Rheedea Vol. 5 (2) : 97—102. 1995

Subdivision and relationships of the Asiatic – Australian genera of Annonaceae[1]

P. J. A. Kessler

Rijksherbarium/Hortus Botanicus, Leiden, P. O. Box 9514, NL-2300 RA Leiden, The Netherlands

Abstract

Although the Annonaceae as a family is well characterized, its subdivision has always been problematic. Classifications are far from being comparable with each other, although all contain valuable elements. Some tribes, especially those containing genera from South America, are very distinct and represent clearcut and well-defined groups of taxa. Asiatic – Australian genera with their reticulate distribution of primitive and advanced characters and parallelism show difficulties for a classification on tribal level. Nevertheless a number of phenetic classifications relying on flower, pollen, fruit and seed characters have been published recently which will help to make sound decisions after monographs of the big Asian general have been completed.

INTRODUCTION

The Annonaceae is a large pantropical plant family which plays an ecologically important role in the lowland forests of Malesia. Of the total of 126 genera only two are represented outside the tropics, namely *Asimina* Adans. and *Deeringothamnus* Small, with *Asinina triloba* (L.) Dunal (American Papaw) reaching the southern most part of Canada. Several tropical species are known to occur in cool and windy high-elevation forests, including *Disepalum pulchrum* (King) Sinclair, *Polyalthia montana* Ridley, *Sageraea thwaitesii* Hook. f. & Thoms., and *Phoenicanthus coriacea* (Thw.) H. Huber (over 1500 m elevation), *Friesodielsia alpina* (Sinclair) Steenis, *Pseuduvaria taipingensis* Sinclair, and some *Goniothalamus* Hook. f. & Thoms., esp. *G. clemensii* Ban, *G. montanus* Mat Salleh, and *G. roseus* Stapf (over 1200 m elevation).

Economically only some South and Middle American species are worth mentioning: *Annona muricata L.* (Soursop, Sirsak in Indonesia), *Annona squamosa L.* (Sugarapple, Sirkaja), and *Annona cherimolia* Miller (Cherimoya) which provide palatable fruits often used in juices. These species are nowadays cultivated for their syncarps all over the tropics and are found regularly in the markets throughout the Malesian region.

1 This paper is to commemorate the 65th birthday of Professor H. Huber, University of Kaiserslautern Germany, who introduced me to plant taxonomy and especially to the Annonaceae.

P. J. A. Kessler

Apocarpous Annonaceae species with edible monocarps are less common and only of local importance. In the Asian region especially some *Uvaria L.* and *Alphonsea* Hook. f. & Thoms. species provide nice fruits and *Stelechocarpus burahol* (Blume) Hook. f. & Thoms. (Kepel) is very much sought after in Java. Unfortunately, as in many other tropical fruits, the edible part in these is thin but very tasty.

The whole family many count between 126 and 130 genera in the world, depending on wide or narrow genus concept. Approximately 50 genera with more than 850 species occur in Austral–Asia compared to about 40 genera with 250 species in Africa or 36 genera with about 600 species in America. Diversity of the Asian Annonaceae is very high, but in contrast to America and Africa, many of the Asian members are climbers. Some of the genera like *Uvaria* L. (110 spp.), *Artabotrys* R. Br. (100 spp.), *Friesodielsia* Steenis and *Fissistigma* Griffith (with more than 60 species each) represent some of the largest genera within the family. All these genera are exclusively lianas, not a single species representing the tree or shrub habit. Other large genera are *Goniothalamus* (Blume) Hook. f. & Thoms. (130 spp.), *Polyalthia* Blume (100 spp.), and *Xylopia* L. (150 spp.); the latter, however, has a pantropical distribution. All species are mainly understorey trees with some exceptions: *Mezzettia parviflora* Becc. may reach 40 m height.

Although the Annonaceae, as a family, are well characterized and supposed to be monophyletic, subdivision and the relationships between genera have always been problematic. This is reflected by the different classifications that have been proposed in systematic treatments.

During the last 20 years some substantial effort has been made to evaluate different character sets of the family as a means for discerning interrelationships and for classifying them accordingly:

- Pollen: studied by Walker (1971, 1972) Le Thomas (1980, 1981), and Morawetz & Waha (1985).
- Chromosomes: studied by Sauer & Ehrendorfer (1984) and Okada & Ueda (1985).
- Leaf venation patterns: studied by Klucking (1986).
- Anatomy of the seeds: Studied by Christmann (1986).
- Morphology of fruits and seeds: studied by van Setten and Koek-Noorman (1992).
- Flower morphology: studied by van Heusden (1992).
- Embryology: studied by Steinecke (1993).

Many of them have attempted to construct large-scale classification of the whole family, usually based on their restricted character sets only. It has been found that they all support each other to a very considerable extent, if only the American genera are concerned. One of

the most famous examples is the Annona-group consisting of the genera *Annona* L., *Anonidium* Engl. & Diels, *Raimondia* Saff. and *Rollinia* A. St. Hil. as well as the Guatteria– and Duguetia–groups which have been accepted by all authors since their creation by Fries (1959). Inaccurate determination of material has been one of the biggest constraints in this type of work, involving evaluation of such data. That is, at least, true for the Asiatic species as revisions of most of the larger genera are not available. Typical examples are the papers of Walker (1971, 1972) and Klucking (1986). Many specimens from Asia cited by these authors actually belong to different, and sometimes even, unrelated genera. This, of course, makes it impossible to interpret the data correctly and I would suggest that more effort should be made to revise or monograph Asiatic Annonaceae.

The Asiatic – Australian genera of Annonaceae are still the least known members of the family although some progress has been made recently.

Revisions of the following Asiatic–Australian genera are now at hand:

I. Already published revisions

Orophea Blume (41 spp., Kessler 1988, 1990)

Disepalum Hook f. (incl. *Enicosanthellum* Ban, 9 spp., Johnson 1989)

Meiogyne Miq. (incl. *Ancana* F. Muell., *Chieniodendron* Tsiang & P. T. Li, *Guamia* Merr., *Oncodostigma* Diels, *Polyaulax* Backer, 9 spp., van Heusden 1994)

Haplostichanthus F. Muell. (incl. *Papualthia* Diels, 6 spp., van Heusden 1994)

Mezzettia Becc. (4 spp., van der Heijden & Kessler 1990)

Anaxagorea A. St. Hil. (2 spp., Maas & Westra 1984)

Platymitra Boerl. (2 spp., Kessler 1988)

Stelechocarpus (Blume) Hook. f. & Thoms. (2 spp., van Heusden 1995)

II. Revisions not yet published, manuscripts almost finished:

Goniothalamus (Blume) Hook. f. & Thoms. (30 spp., Bornean species only, Kamarudin Mat Salleh)

Alphonsea Hook. f. & Thoms. (24 spp., Kessler)

Cyathostemma Griffith (incl. *Tetrapetalum* Miq., 10 spp., Utteridge)

Sageraea Dalz. (6 spp., van Heusden)

These studies contribute to about 16% of the total number of species belonging to small and very small genera. But, when it comes to Austral–Asian taxa, lack of proper and adequate

taxonomic data continues to be a cause for worry for taxonomists involved in their classification, both at suprageneric and infrageneric levels. Even as generic synonymy continues to add to their woes, difficult genera like *Polyalthia* Bl., *Uvaria* L., *Desmos* Lour., *Pseuduvaria* Miq., and *Mitrephora* (Blume) Hook. f. & Thoms. have not yet received the taxonomic attention that they deserve.

In short, the circumscription, characterisation, and phylogenetic relationship of the various genera are yet to be clearly delineated. Even as some of them are clearly monophyletic, some others seem to be paraphyletic. But this requires further confirmation. I am aware that it is far too early to propose an infrafamilial classification of the Annonaceae in Austral–Asia. Yet, I am providing here a tentative, informal classification of the various perceived groupings in the family, in the hope that it will help future course of taxonomic research and monographic studies.

CLASSIFICATION

1. Uvaria group:
Mainly climbers; hairs stellate or caespitose; flowers leaf-opposed; sepals valvate; petals imbricate; ovules several, lateral.

Included genera: *Uvaria* L. *Cyathostemma* Griff. (incl. *Tetrapetalum), Ellipeia* Hook. f. & Thoms., *Ellipeiopsis* R. E. Fries, *Rauwenhoffia* R. Scheffer, *Anomianthus* Zoll.; probably also *Sageraea* Dalz., *Stelechocarpus* (Blume) Hook. f. & Thoms. Doubtfully attached genera: *Dendrokingstonia* (Hook. f. & Thoms.) Rauschert, *Dasoclema* Sinclair.

2. Desmos group:
Climbers or trees; hairs simple or absent; sepals and petals valvate, both whorls of petals more or less equal in size; ovules many to one, lateral, rarely basal (*Polyalthia* sect. *Monoon* (Miq.) Blume).

Included genera: *Desmos* Lour., *Dasymaschalon* (Hook. f. & Thoms.) Dalla Torre & Harms, *Polyalthia* Bl., *Sphaerothalamus* Hook. f., *Monocarpia* Miq., *Enicosanthum* Becc., *Woodiellantha* (Merr.) Rauschert; probably also *Meiogyne* Miq. (incl. *Guamia, Polyaulax, Oncodostigma, Chieniodendron, Ancana).*
Doubtfully attached genus: *Haplostichanthus* F. Muell. (Incl. *Papualthia*).

3. Xylopia group:
Trees or climbers; hairs simple; sepals and petals valvate, petals spoon-shaped, concave base coherent around the reproductive organs.

Included genera: *Xylopia, Artabotrys* R. Brown, *Cyathocalyx* Champ. ex Hook. f. & Thoms., *Drepananthus* Maingay ex Hook. f. & Thoms., *Anaxagorea* A. St. Hil.; probably also *Marsypopetalum* Scheffer.

4. Pseuduvaria group:
Trees or climbers; hairs simple or absent; inner petals mitriform, clawed; stamens numerous, connective with a truncate dilated apex.

Included genera: *Pseuduvaria* Miq., *Mitrephora* (Blume) Hook. f. & Thoms., *Goniothalamus* (Blume) Hook. f. & Thoms., *Richella* A. Gray, *Schefferomitra* Diels, *Melodorum* Lour., *Friesodielsia* Steenis, *Oreomitra* Diels, *Petalolophus* Schumann; probably also *Popowia* Endl., *Neo-uvaria* Airy-Shaw, *Trivalvaria* Miq., *Phaeanthus* Hook. f. & Thoms., *Mitrella* Miq., *Pyramidanthe* Miq., *Fissistigma* Griffith.

5. Miliusa group:
Trees; hairs simple or absent; sepals and petals valvate; stamens few, connective without prolonged specialized apex; carpels few.

Included genera: *Miliusa* Leschen. ex A. DC., *Orophea* Blume, *Mezzettiopsis* Ridley, *Phoenicanthus* Alston, *Alphonsea* Hook. f. & Thoms., *Platymitra* Boerl.; probably also *Mezzettia* Becc.

Genera that can not be accommodated in any of the groups:
Cananga Hook. f. & Thoms., *Fitzalania* F. Muell., *Disepalum* Hook. f.

It is obvious that the classification of the Annonaceae is currently in a state of flux, as the older systems based primarily upon perianth morphology are amended using a wider array of features. The available data especially from flower morphology, pollen, fruit, seed morphology, and seed anatomy as well as embryology do not support a single classification for the whole family, as many Asiatic–Australian genera show enormous amount of reticulate distribution of primitive and advanced characters and parallelism, which make it difficult to assess evolutionary relationships between the taxa (Kessler 1993). May I stress again that without revising especially the large Austral–Asiatic genera we will not be able to unravel the complex systematics of this family.

Acknowledgements

This paper has been presented in a slightly different form at the Third International Flora Malesiana Symposium 1995 at Kew. I would like to thank the organisers for their kind invitation. Dr. M. M. J. Van Balgooy (L) and P. Bygrave (K) provided me with some additional information. Dr. V. V. Sivarajan (Calicut) critically read an early version of the manuscript.

Literature cited

Christmann, M. 1986. Beiträge zür Histologie der Annonaceen–Samen. *Bot. Jahrb. Syst.* 106 : 379–390.

Fries, R. E. 1959. Annonaceae in A. Engler & K. Prantl (Eds.) *Die naturlichen Pflanzenfamilien* edn. 2nd 17A. Duncker & Humblot, Berlin.

Heijden, E. van der & Kessler, P. J. A. 1990. Studies on the tribe Saccopetaleae (Annonaceae) – III. Revision of the genus *Mezzettia* Beccari. *Blumea* 35 : 217–288.

Heusden, E. C. H. van 1992. Flowers of Annonaceae: Morphology, classification, and evolution. *Blumea, Suppl.* 7 : 1–218.

Heusden, E. C. H. van 1994. Revision of *Meiogyne* (Annonaceae). *Blumea* 38 : 487–511.

Heusden, E. C. H. van 1994. Revision of *Haplostichanthus* (Annonaceae). *Blumea* 39 : 215–234.

Heusden, E. C. H. van 1995. Revision of the Southeast Asian genus *Stelechocarpus* (Annonaceae). *Blumea* 40 : 407–416.

Johnson, D. M. 1989. Revision of *Disepalum* (Annonaceae). *Brittonia* 41 : 356–378.

Kessler, P. J. A. 1988. Revision der Gattung *Orophea* Blume (Annonaceae). *Blumea* 33 : 1–80.

Kessler, P. J. A. 1988. Studies on the tribe Saccopetaleae (Annonaceae) – I. Revision of the genus *Platymitra* Boerlage. *Blumea* 33 : 471–476.

Kessler, P. J. A. 1990. Studies on the tribe Saccopetaleae (Annonaceae) – II. Additions to the genus *Orophea* Blume. *Blumea* 34 : 505–516.

Kessler, P. J. A. 1993. Annonaceae. In Kubitzki, K. et al. (Eds.). *The families and genera of vascular plants*. Springer, Berlin.

Klucking, E. P. 1986. *Leaf venation patterns 1 :* Annonaceae. Cramer, Berlin, Stuttgart.

Le Thomas, A. 1980. Ultrastructural characters of the pollen grains of African Annonaceae and their significance for the phylogeny of primitive angiosperms I. *Pollen and Spores* 22 : 267–342.

Le Thomas, A. 1981. Ultrastructural characters of the pollen grains of African Annonaceae and their significance for the phylogeny of primitive angiosperms II. *Pollen and Spores* 23 : 5–36.

Maas, P. J. M. & Westra, L. Y. Th. 1984. Studies in Annonaceae. II. A monograph of the genus *Anaxagorea* A. St. Hil. *Bot. Jahrb. Syst.* 105 : 73–134.

Morawetz, W. & Waha, M. 1985. A new pollen type, C–banded and fluorescent counterstained chromosomes and evolution in *Guatteria* and related genera (Annonaceae). *Pl. Syst. Evol.* 150 : 119–141.

Okada, H. & Ueda, K. 1984. Cytotaxonomical studies on Asian Annonaceae. *Pl. Syst. Evql.* 104 : 165–177.

Sauer, W. & Ehrendorfer, F. 1984. Notes on the karyosystematics of Annonaceae. *Pl. Syst. Evol.* 146 : 47–55.

Setten, A. K. van & Koek–Noorman, J. 1992. Fruits and seeds of Annonaceae: Morphology and its significance for classification. *Bibl. Bot.* 142 : 1–101.

Steinecke, H. 1993. Embryologische, morphologische und systematische Untersuchungen ausgewanlter Annonaceae. *Diss. Bot.* 205 : 1–237.

Walker, J. W. 1971. Pollen morphology, phytogeography and phylogeny of the Annonaceae. *Contrib. Gray Herb.* 202 : 3–131.

Walker, J. W. 1972. Contributions to the pollen morphology and phylogeny of the Annonaceae II. *Bot.. J. Linn. Soc.* 65 : 173–178.